

Additional Observations on the Mode of Fecundation in Orchideæ.

Read June 5, 1832.

THE following additions to the Paper, which was communicated to the Society in November last, on the Sexual Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ, relate entirely to the former family.

In the essay itself I had ascertained from the examination of a considerable number of species belonging to different tribes of Orchideæ, that in the expanded flower of this family, however long it had remained in that state, no appearance whatever existed of those tubes which form the mucous cords, either in the tissue of the stigma or in the cavity of the ovarium, anterior to the application of the pollen to the stigma; and that in all cases where pollen had been applied to that organ and enlargement of the ovarium had followed, the mucous cords were to be found.

From these facts I had concluded that the tubes forming the cords were entirely and directly produced from the grains of pollen; and hence I accounted for the cohesion of the pollen into masses, and its frequent application in that state to the stigma.

Some cases, however, in which a few lobules or even grains of pollen only were observed on the stigmata of impregnated flowers, had led me to express myself doubtfully on this point. And since my paper was read, I have had opportunities of making several observations and experiments which prove that the application of a very small portion of a pollen mass to the stigma is sufficient for the production of mucous cords of the ordinary size in the cavity of the ovarium.

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My observations on this point and on the gradual production and descent of these cords have been made chiefly on *Bonatea speciosa*, perhaps the most favourable subject for such experiments in the whole family.

My first observation on *Bonatea* related to the probability of a single insect impregnating several or even many flowers with one and the same mass of pollen.

To effect this, it is only necessary that the viscidility of the retinaculum or gland with which the pollen mass becomes inseparably connected, and by means of which the mass is removed from its cell and adheres to the insect, should exceed that of the surface of the stigma, and that the viscidility of the stigma should be sufficient to overcome the mutual cohesion of the lobules composing the mass.

These different degrees of viscidility are very manifest in *Bonatea speciosa*, in which, imitating the supposed action of the insect, I have succeeded in impregnating most of the flowers of the spike with a single pollen mass. I believe they exist also in the greater number of Ophrydeæ, as well as in many Neotteæ and Arethuseæ.

But even in Ophrydeæ they are not universally met with, a very remarkable exception existing I believe in the whole genus Ophrys, in which the resemblance of the flower to an insect is so striking, and in which also the retinacula, whose viscidility hardly equals that of the stigma, are included and protected by concave processes of the upper lip of that organ.

It may also be remarked, that in the genus Ophrys impregnation is frequently accomplished without the aid of insects, and in general the whole pollen mass is found adhering to the impregnated stigma. Hence it may be conjectured, that the remarkable forms of the flowers in this genus are intended to deter not to attract insects, whose assistance seems to be unnecessary,

cessary, and the action of which, from the diminished viscosity of the retinaculum, might be injurious. On this subject I will also hazard another remark, that the insect forms in Orchideous flowers, resemble those of the insects belonging to the native country of the plants.

The next object I had in view was to determine the first appearance and progress of the mucous tubes.

My observations on the *origin* of these tubes are not altogether satisfactory.

It appeared, however, in *Bonatea*, which was also the plant most particularly examined, that they first become visible soon, but not immediately, after the production of the pollen tubes from the lobules or grains of the mass applied to the stigma; and that their earliest appearance is in the tissue of the stigma, in the immediate vicinity of the pollen tubes, from which they are with difficulty distinguishable, and only by their being less manifestly or not at all granular in their surface or contents, and in general having those interruptions in their cavity, which I have termed coagula, and which I have never yet met with in tubes actually adhering to the grain of pollen.

But even these characters, in themselves so minute, might be supposed to depend on a difference in the state of the contents of the pollen tube, after it has quitted the grain producing it. It is possible therefore that the mucous cords may be entirely derived from the pollen, not however by mere elongation of the original pollen tubes, but by an increase in their number, in a manner which I do not attempt to explain.

The only other mode in which these tubes are likely to be generated, is by the action of the pollen tubes on the coagulable fluid, so copiously produced in the stigma at the only period when impregnation is possible.

The obscurity respecting the origin of these mucous tubes
does

does not however extend to their gradual increase and progress, both of which may be absolutely ascertained.

In *Bonatea* they are, in the first stage of their production, confined to the stigma, with the proper tissue of which they are more or less mixed. Soon after they may be found on the anterior protected surface of the style, at first in small numbers; but gradually increasing, they form a mucous cord of considerable size, in which very few or none of the utriculi of the stigma are observable. This cord, which is originally limited to the style, begins, though sometimes not until several days have elapsed, to appear in the cavity of the ovarium, where it divides and subdivides in the manner I have described in my paper, its descent being gradual until the cords nearly equal the length of the placenta, to which they are parallel and approximated.

That these cords are not in any degree derived from those portions of the walls of the cavity of the ovarium, to which they are closely applied, and which I have termed the conducting surfaces, is manifest from the identity in state of those surfaces before and after the production of the cords.

In *Bonatea* the first evidence of the action of the pollen consists in the withering of the stigma; a similar decay of the greater part of the style soon follows, and the enlargement of the ovarium generally begins before the withering of the style is completed. When the enlargement of the ovarium is considerable, and the mucous cords are carefully formed in its cavity, a corresponding enlargement of the ovula takes place, and the nucleus becomes first visible.

I have no satisfactory observations in *Bonatea* respecting any tubes going off from these cords and mixing with the ovula; but in *Orchis Morio* I have repeatedly and very clearly observed them scattered in every part of the surface of the placenta, and in not a few cases have been able to trace them into the aperture

ture of the ovulum, to which they adhere with considerable firmness*.

At what period they reach the foramen of the testa, whether before or immediately after the first faint appearance of the nucleus, I have not yet been able to determine. That the tubes thus traced to the foramen of the ovulum are of the same nature as those which I have called mucous tubes, and not those directly produced by the pollen, is proved by their exact agreement with the former in every respect, except in their being remarkably and irregularly flexuose, apparently from the numerous obstacles they have to overcome after leaving the cords and beginning to mix with the ovula; for in the cords themselves, where the course of the tubes is not at all impeded, they are very nearly or altogether straight.

The two most important facts stated in the present communication are; *first*, the production of tubes not directly emitted from the grains of pollen, but apparently generated by them; and, *secondly*, the introduction of one or sometimes more than one of those tubes into the foramen of the ovulum, the point corresponding with the radicle of the future embryo.

The principal points remaining to be examined, and which we may hope, by careful investigation, to ascertain, are the precise state of the ovulum at the moment of its contact with the tube, and the immediate changes consequent to that contact.

* Since these additional observations were read, I have found in several other Orchideæ, especially *Habenaria viridis* and *Ophrys apifera*, tubes scattered over the surface of the placenta, and not unfrequently inserted, in like manner, into the apertures of ovula.

Supplementary Note.

SINCE the Paper on Fecundation in Orchideæ and Asclepiadeæ was read before the Society, and a Pamphlet containing all its more important statements was distributed in the beginning of November 1831*, two essays have appeared on the same subject. The first on both families by M. Adolphe Brongniart, in the numbers of the *Annales des Sciences Naturelles* for October and November 1831, but which were not published until January and February 1832: the second, by Dr. Ehrenberg, on Asclepiadeæ alone, in the Transactions of the Royal Academy of Sciences of Berlin, before which it was read in November 1831.

M. Brongniart's statements respecting ORCHIDEÆ to a great extent agree with those of my essay. They differ, however, in the following important points :

1st, He does not seem to be aware of the operation of insects in the fecundation of this family.

2ndly, He considers the mucous cords in the cavity of the ovarium (first seen by M. Du Petit Thouars, with whose observations he seems to be entirely unacquainted,) as a continuation of the tissue of the stigma and style, and as existing before the application of the pollen to the female organ.

And 3rdly, He supposes that the male influence reaches the ovula in Orchideæ before the inversion of the nucleus ; an opinion founded, as it seems, on his observations on *Epipactis*, in which, as well as in some other genera of the order, this is the state of the ovulum in the expanded flower.

In ASCLEPIADEÆ M. Brongniart's observations, made chiefly in *Asclepias amæna* and *Gomphocarpus fruticosa*, accord with my statements as far as relates to the application of the more convex

* I may also refer to an excellent abstract of the Paper which appeared on the 1st of December 1831 in the *Philos. Mag. and Annals of Philosophy*.

edge of the pollen mass to the base of the stigma, its consequent dehiscence, the protrusion of the pollen tubes, and their penetration into the cavity of the style.

The chief differences are,

1st, His not even suspecting the agency of insects in the fecundation of this family, and particularly in the plants examined by him, in which I have regarded their assistance as absolutely necessary.

2ndly, In his assuming that the pollen mass in these two genera of Asclepiadeæ is ruptured, and comes in contact with the base of the stigma without leaving the cell of the anthera.

3rdly, His conjecturing that the secretion visible in the expanded flower on the angles of the stigma after removing the glands, is absorbed by the glands and conveyed through their arms or processes to the pollen mass, which it excites to the production of pollen tubes.

Dr. Ehrenberg on the subject of Asclepiadeæ, repeats, with some slight modifications, his former statements quoted in my paper, and illustrates them by figures. In addition, he suspects that the pollen masses (which with Professor Link he regards as the true anthera, and the cells in which they are lodged as processes of the perigonium,) are not originally distinct from the glands of the stigma, regarded by him as the filaments of his supposed anthera.

The central pentangular body he considers as the stigma, but he has no observations on the mode in which the pollen is applied to it.

And lastly, His original statement respecting the grains of pollen is so far modified, that he now believes them to be in the early stages without tubes or *boyaux*, which, according to him, make their appearance at the period of impregnation.